

Effect of Synthetic Pheromone on Gypsy Moth (Lepidoptera: Lymantriidae) Trap Catch and Mating Success Beyond Treated Areas

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ABSTRACT Racemic disparlure sprayed at doses of 37 to 75 g/ha (AI) for mating disruption of gypsy moths, *Lymantria dispar* (L.), interfered with male moth search behavior outside of treated plots. Counts of feral male moths in pheromone-baited traps and the number of recaptured laboratory-reared moths gradually increased with increasing distance from treated areas. In most cases this effect was observed up to 250 m from treated plots. However, in one location it extended to 600 m along a narrow valley. The proportion of tethered females that mated during 1-d exposure increased gradually with increasing distance from treated plots. The relationship between male moth capture rates in pheromone traps and mating success of tethered females near treated plots was the same as the one observed in previous studies in pheromone-free areas.

KEY WORDS gypsy moth, disparlure, pheromone, mating disruption, release-recapture, *Lymantria dispar*

MATING DISRUPTION IS the use of synthetic sex attractants to disorient males and subsequently decrease the number of fertilized eggs laid by females (Cardé and Minks 1995). This method of population control is increasingly used against the gypsy moth, (*Lymantria dispar* L.), (Leonhardt et al. 1996, Reardon et al. 1998, Sharov et al. 2002a), which is a serious pest of hardwood forests in northeastern United States (Doane and McManus 1981, Twardus 1994). The gypsy moth was first introduced into North America in 1869 near Boston. Since that time, its populations has reached Virginia and North Carolina in the south, Indiana and Illinois in the west, and Wisconsin in the north (Liebhold et al. 1992, Sharov et al. 1999). However, only one-third of the North American forests containing susceptible host trees have become infested (Liebhold et al. 1997). To slow the expansion of gypsy moth populations into these areas, the USDA conducts a national Slow-the-Spread (STS) program to eradicate isolated infestations in areas beyond the moving population front (Leonard and Sharov 1995, Sharov et al. 2002a).

The gypsy moth sex pheromone is (Z)-7,8-epoxy-2-methyloctadecane, or disparlure (Bierl et al. 1970). The (+) enantiomer of disparlure is considerably more attractive to gypsy moth males than the racemic disparlure (Plimmer et al. 1977, Cardé et al. 1977, Miller et al. 1977). Mating disruption treatments use racemic disparlure because of its lower cost and be-

cause it disrupts mating as effectively as the (+) enantiomer (Plimmer 1982, Kolodny-Hirsch and Schwalbe 1990). The (–) enantiomer of disparlure is not attractive but it inhibits the response of males to (+) disparlure (Yamada et al. 1976, Cardé et al. 1977, Miller et al. 1977).

To locate a mate, gypsy moth males follow pheromone trails on a large spatial scale, but then switch to a local search on tree boles where females are calling (Richerson et al. 1976a, Cardé and Hagaman 1984). Richerson et al. (1976a) observed vertical flight of males near tree boles in areas treated with disparlure. They suggested that mating disruption is caused by a behavioral switch from a long-range following of relatively weak pheromone plumes to a short-distance search on boles even in areas where females are not present. Richerson et al. (1976a) thought that sight might be important in short-range search, but experiments of Charlton and Cardé (1990) indicated that sight does not help males to find a female. Probably the goal of local search on boles is to find a strong plume of pheromone.

Attempts to use disparlure to disrupt gypsy moth mating began in 1971 (Doane and McManus 1981), and operational applications have occurred since 1979 (Kolodny-Hirsch and Schwalbe 1990). Among several types of dispensers that have been tested for gypsy moth mating disruption, plastic pheromone flakes (Disrupt II, Hercon Environmental, Emigsville, PA) are currently the only product that is commercially available. Flakes release 30 to 50% of their disparlure content over a 6-wk period (Leonhardt et al. 1996,

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Thorpe et al. 1998). A single application is sufficient to prevent mating during the entire period of moth flight. Field tests with various doses showed that 75 g per hectare was sufficient to disrupt mating in gypsy moth populations (Webb et al. 1988, Reardon et al. 1998). A single application of disparlure postponed the growth of gypsy moth populations by 1 yr, and annual applications kept population densities at low levels for 5 yr (Reardon et al. 1998).

Mating disruption works best at low population densities (Schwalbe et al. 1983, Webb et al. 1990). It is not suitable for suppression of outbreak populations, but can be used to eradicate small isolated colonies with low population density. The treatment of isolated colonies is an important tactic in the USDA Forest Service Slow-the-Spread (STS) program (Leonard and Sharov 1995, Sharov et al. 2002a, b). Gypsy moth populations spread via establishment of isolated colonies ahead of the moving front (McFadden and McManus 1991). If not treated these colonies grow, coalesce and eventually contribute to the progression of the population front (Sharov and Liebhold 1998). The strategy of the STS project is to detect and eradicate or suppress isolated colonies at a very early stage. The advantage of using mating disruption in the STS project is that it does not affect nontarget species and hence has a lower environmental risk than pesticides or *Bacillus thuringiensis* (Berliner) variety *kurstaki*. Mating disruption with disparlure at 37.5 to 75 g/ha appeared more efficient than double applications of *B. thuringiensis* at 24 to 30 BIU/ha (Sharov et al. 2002b). The area treated with disparlure in the STS project increased to ≈ 200 thousand acres in 2001 (Sharov et al. 2002a).

The use of mating disruption against low-density isolated populations of the gypsy moth in the STS project provoked several questions that require additional research. One practical question is how far beyond the edge of treated areas is mating disrupted. Currently, disparlure is applied uniformly over the entire area in the same way as pesticides. However, if mating can be disrupted at some distance away from the site of application, then it would be possible to leave gaps in the coverage without loss of the overall effect. In this paper we present results of a series of experiments designed to confirm the distant effect of pheromones, and to determine its extent in space.

Materials and Methods

Experimental Plots and Treatments. In 2000, experimental plots were located near Millboro Springs (Bath Co., VA), and in 2001, experiments were conducted near Goshen (Rockbridge Co., VA), at the Buckingham-Appomattox State Forest (Buckingham and Appomattox Co., VA), and at the Cumberland State Forest (Cumberland Co., VA). Locations at Millboro Springs and Goshen are in the ridge-valley region of the Appalachian Mountains, and the Buckingham-Appomattox and Cumberland locations are in a relatively flat Piedmont area. All locations were at the front of the advancing populations of the gypsy moth.

Moth counts in pheromone traps in experimental locations in the year preceding our experiments were 21 to 151 moths per trap near Millboro Springs, 82 to 229 moths per trap near Goshen, 2 to 12 moths per trap in the Buckingham-Appomattox State Forest, and 42 to 98 moths per trap in the Cumberland State Forest.

Plots were treated aerially with racemic disparlure in one of two formulations. Pheromone flakes (Disrupt II, Hercon Environmental, Emigsville, PA) are 1×3 mm layered plastic dispensers that are mixed with a sticker (Gelva-2333, Solutia Inc. Springfield, MA) and applied aerially using special equipment (Reardon et al. 1998). Experimental microcapsules (3 M Canada Co., London, Ontario, Canada) are 5 to 100 microns in diameter; they were mixed with water and applied using conventional spraying equipment. Doses of disparlure in our experiments varied from 37.5 to 75 gAI/ha. These doses were demonstrated previously to be effective against medium- and low-density populations (Reardon et al. 1998).

Near Millboro Springs, six 25-ha square plots (M1-m6) separated by ≈ 1 km were selected for disparlure treatment (Fig. 1). These blocks were placed along the same road in a narrow valley between two ridges, Walker Mountain and Sideling Hill, at an elevation of 600–730 m. The elevation at the tops of the ridges was 900 to 950 m. Plots M1, M2, M4, and M6 were sprayed on 27 through 29 June 2000 with pheromone flakes at doses of 75 g/ha (M2 and M4) and 37 g/ha (M1 and M6). Plots M3 and M5 were treated on 29 June 2000 with three M microcapsules at a dose of 75 g/ha.

Two 25-ha square plots, one in the Buckingham-Appomattox State Forest (BA1) and another in the Cumberland State Forest (C1) were treated on 12 June 2001 with three M microcapsules at a dose of 75 g/ha. The elevation in these plots was 700 and 215 m, respectively. These plots were part of a larger dose-response study. They were separated by > 2 km from other plots; hence, the experiment was not affected by other treatments.

One 1000×500 m plot was located near Goshen (G1) and another in the Buckingham-Appomattox State Forest (BA2). Plot G1 was in a broad valley at an elevation of 450 to 500 m, with nearby ridges 850 to 900 m high. Plot BA2 was at an elevation of 300 m. Both plots were treated on 11 June 2001 with Disrupt II flakes and a sticker at an average dose of 37 g/ha and with 90-m gaps between treated swaths, each 30 m wide.

All treatments were applied from a fixed-wing airplane. A differentially-corrected global positioning system (DGPS) was used for aircraft navigation and to guide the application.

Effect of Disparlure on Trap Catch of Feral Male Moths Outside of Treated Areas. To test the long-range effect of sprayed disparlure on the capture rates of feral male moths, we placed traps at various distances from treated plots. We used USDA milk-carton traps baited with 500 mg of (+)-disparlure in twine dispensers (Schwalbe 1981, Leonhardt et al. 1992). Trap coordinates were measured using DGPS. Traps

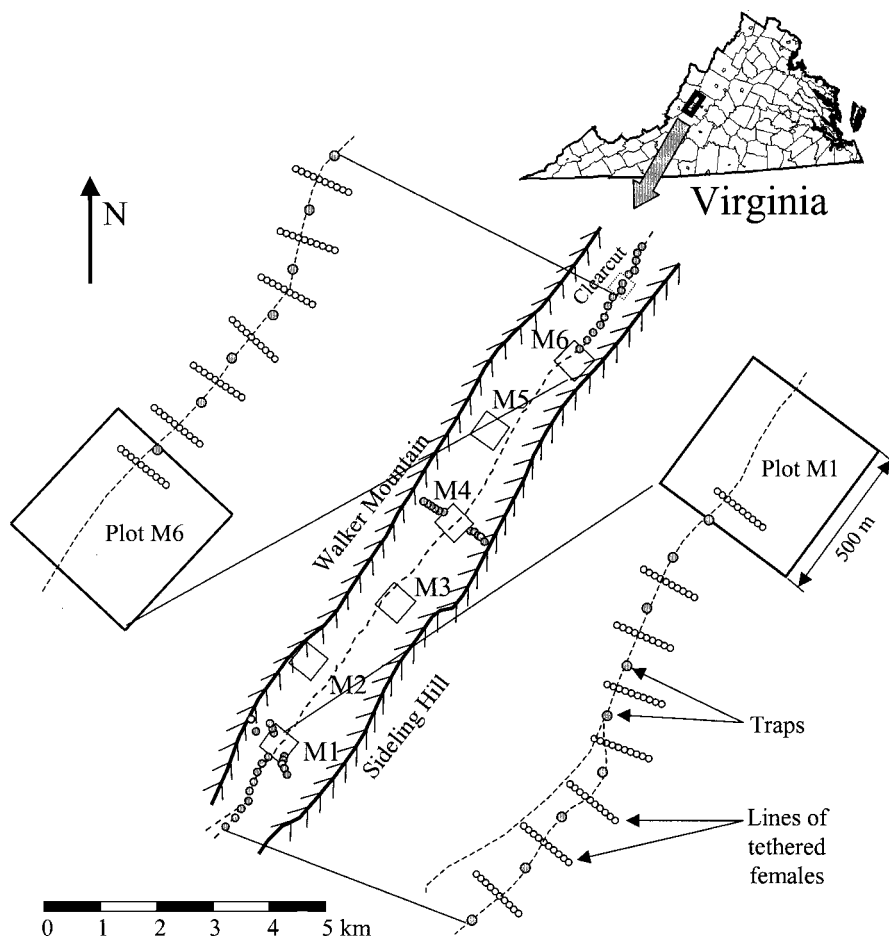


Fig. 1. Map of experimental plots treated in 2000 with gypsy moth mating disruptant (squares M1-m6) and pheromone traps (gray circles) near Millboro Springs, VA. Lines of tethered females (empty circles) near plots M1 and M6 are shown at a higher resolution.

were checked 1 to 2 times per week and moths were removed and counted.

On 7 July 2000, lines of traps separated by 200 m were placed along the road to the south-west from plot M1 and to the north-east from block M6 (Fig. 1). Also, four short lines of traps separated by ≈ 100 m were placed on the slopes of the ridges on either side of plots M1 and M4.

On 1 June 2001, two lines of traps were placed to the east and south of plot G1. Each line had four groups of traps at target distances of 0, 100, 200, 500, and 1000 m from plot G1. The actual location of traps was adjusted to satisfy conditions of good habitat for the gypsy moth and accessibility. Thus, actual distances deviated slightly from planned values. Each group had four traps at 25 m to the north, south, east, and west of center.

The relationship between moth counts in traps (N) and distance from the nearest treated plot (x) was modeled as

$$\ln(N + 1) = a \cdot [1 - \exp(-3x/b)], \quad [1]$$

where parameter a is the maximum of log moth counts and b is the range of the disparlure effect determined using nonlinear regression (least square method). Traps located in the treated area ($x < 0$) were not used in the nonlinear regression.

To test the difference in moth counts between groups of traps located at various distances from the treated area we used a General Linear model procedure with Tukey adjustment for multiple comparison of mean values (SAS 1996; Proc GLM). Log-transformed total moth count in traps for the entire flight period, $\ln(N+1)$, was modeled as a function of distance class from the treated area and line of traps, without the inclusion of factor interactions. Distance classes were: (1) < 50 m, (2) 50-150 m, (3) 150-250 m, (4) 250-600 m, (5) 600-1200 m, and (6) > 1200 m from the boundary of the treated area.

Effect of Disparlure on the Recapture Rate of Released Male Moths Outside of Treated Areas. A number of release-recapture sites were located at varying distances from the treated plots. The same number of

male gypsy moths was released in each site, and the effect of distance from treated plot on the number of recaptured individuals was tested. Male moths were released from the center of the site and four pheromone traps were placed at 25 m to the north, south, east, and west.

Male gypsy moths were shipped as pupae from the USDA APHIS Otis Methods Development Center, MA, twice a week. They were kept in paper cups before the start of moth emergence and then placed into release cups in the field. Release cups were 900 ml laminated paper cups with plastic lids. Several openings were cut at mid-height of these cups so that emerging males could easily get out. Emergence cups were stapled to small trees at a height of 1 to 1.5 m. Tanglefoot (The Tanglefoot Co., Grand Rapids, MI) glue circles around tree trunks protected cups from ant predation from below and above. Fluorescent powder dye was added to cups to mark emerging male moths. Each week the same number of pupae (from 100 to 200) were placed in all release sites and the traps were checked. Male moths were removed from traps and stored in the freezer. Later they were examined under the microscope with UV light. Released moths were distinguished by the presence of fluorescent powder on wings, antennae, or body.

In 2000, we placed release-recapture sites in four lines along and across the valley after the end of the natural moth flight season. The distance from these sites to the nearest treated area varied from 0 to 1.6 km. Traps were checked from 31 July to 14 August. Moth catches were low in the first week; thus we analyzed results only for the last 2 weeks.

In 2001, we placed six lines of release-recapture sites: two lines near plot G1, two lines near plot BA2, and single lines near plots BA1 and C1. Each line had five release-recapture sites at target distances of 0, 100, 200, 500, and 1000 m from the area treated with disparlure except plot C1 where release-recapture sites were at distances of 100, 400, 500, and 1000 m. The location of sites was adjusted to satisfy conditions of good habitat for the gypsy moth and ease of accessibility. Recapture of moths continued from 11 June to 6 July near plot G1, from 11 June to 31 July near plot BA2, from 29 June to 31 July near plot BA1, and from 22 June to 31 July near plot C1. The experiment at plot BA2 was interrupted from 22 to 29 June because of logistic problems.

For statistical analysis we used the GLM procedure with Tukey adjustment for the multiple comparison of mean values (SAS 1996; Proc GLM). Log-transformed total moth counts from four traps at each site, $\ln(N+1)$, was modeled as a function of distance class from the treated area, release-recapture line, and week, without factor interactions. Distance classes were: (1) < 50 m, (2) 50-150 m, (3) 150-250 m, and (4) > 250 m from the boundary of treated area.

Effect of Disparlure on Mating Success of Females Outside of Treated Areas. Mating success was evaluated by exposing tethered laboratory-reared virgin females on tree boles for 1 d. Females were shipped twice a week as pupae from the USDA, APHIS, Otis

Methods Development Center, MA. They were kept in paper cups until moth emergence, tethered with a 15 cm long thread tied around the base of a forewing, and placed on tree boles (Sharov et al. 1995). Tethering was important because females often search for refuges after fertilization (Doane 1976) and may be lost. To reduce ant predation, tethered females were surrounded by a band of Tanglefoot glue. Bird predation was negligible. Fertilization of females was detected using two methods: (1) by dissection and analysis of the spermatheca and (2) by analysis of egg embryonation. Females were dissected if they had already laid an egg mass or if they were not healthy at collection time (e.g., damaged by ants). We used a fast dissection method in which the last abdominal segment was pulled away by forceps (Sharov et al. 1995). Usually, the spermatheca can be pulled out. In fertilized females, the spermatheca is white and is full of sperm; in unfertilized females, it is transparent and empty. In some cases sperm were present only in the basal part of spermatheca. If sperm were not found in the spermatheca but an egg mass was present, then these egg masses were kept for 1 to 2 mo and checked for the presence of embryonated eggs. Some egg masses laid by females that had sperm in their spermatheca were also analyzed for embryonation. Out of 58 females whose fertilization status was determined by both methods, five produced embryonated eggs but no sperm were detected (apparently the amount of sperm was too low to allow detection). These five females were considered fertilized. Other females that were healthy but did not lay an egg mass at collection time were kept in paper bags for subsequent oviposition.

All females were classified into the following five categories: (1) obviously fertilized if sperm were present in the spermatheca or >2 eggs were embryonated; (2) obviously unfertilized if no eggs became embryonated or if no sperm were found in the spermatheca of a female that did not lay an egg mass; (3) possibly fertilized if they had only one or two embryonated eggs; (4) possibly unfertilized if a female was healthy at collection time but did not lay any eggs; and (5) undetermined if no eggs were laid and a female was either not collected or was not healthy at the time of collection and dissection was not successful. Females that had only one or two embryonated eggs were not considered obviously fertilized because an egg might accidentally be transferred to another egg mass during analysis. Females that die without laying any eggs are probably unfertilized because normal egg laying behavior is suppressed in virgin females (Doane 1968). The proportion of fertilized females was determined using two methods: (1) including only those individuals that were clearly fertilized or unfertilized, $N_1 / (N_1 + N_2)$, and (2) including also those individuals whose fertilization status was not clear, $(N_1 + N_3) / (N_1 + N_2 + N_3 + N_4)$, where N_i is the number of females in the i -th category.

Lines of tethered females, 10 females per line separated by 15 to 20 m, were deployed at 200 m intervals to the north-east of block M1 (seven lines of females)

and to the south-west from block M6 (eight lines of females) (Fig. 1). The lines of females were placed between pheromone traps, so that the distance from the females to the nearest trap was 100 m. Females were deployed on tree boles every day from 17 to 20 July, and collected on the next day. The proportion of fertilized females was determined using cumulative data from all 4 days of the experiment, and was compared with the average number of moths captured during the same 4 days in the nearest two traps at both sides of the line (Fig. 1).

The proportion of mated females P per day was modeled by:

$$P = 1 - \exp(-s \cdot M), \quad [2]$$

where M is male moth catch in a trap per day and s is a parameter, which is equal to the ratio of probability of a male to copulate with a female to the probability of entering a trap with synthetic pheromone (Sharov et al. 1995). Below it is called as "relative search rate." Parameter s was estimated using the least square method. Parameter values for different data sets were compared with Student statistics

$$t = |s_1 - s_2| / \sqrt{SE_1^2 + SE_2^2}$$

with $df = \nu_1 + \nu_2$, where s_i is an estimate of parameter s , SE_i is the standard error for s_i , and ν_i = df in data set i .

Results and Discussion

Effect of Disparlure on Trap Catch of Feral Male Moths Outside of Treated Areas. In 2000, numbers of moths captured in traps increased with increasing distance from the nearest treated plot in trap lines along the valley and across the valley (Fig. 2). These figures show log-transformed, $\ln(N + 1)$, total moth counts in traps from seven June to four August as examples. All lines of traps exhibited a similar relationship between log moth capture and distance from the nearest treated plot. Low moth counts in two traps shown by arrows in Fig. 2B correspond to the clearcut in Fig. 1. These two points were not used in statistical analysis.

Nonlinear regression (equation 1) indicates a significant effect of distance from the nearest treated plot on moth counts in lines of traps both along the valley (Fig. 2A) ($R^2 = 0.70$; $F = 45$; $df = 1, 17$; $P < 0.001$), and across the valley (Fig. 2B) ($R^2 = 0.61$; $F = 26$; $df = 1, 17$; $P < 0.001$). The range of disparlure effect on moth capture was greater along the valley ($b = 1899 \pm 189$ m, \pm SE) than across the valley ($b = 312 \pm 66$ m). Apparently, disparlure plumes disperse farther along the valley than up the slopes.

The GLM analysis confirmed the significant effect of distance from treated area on moth counts in lines of traps both along the valley and across the valley (Table 1; Fig. 3). In lines of traps along the valley, mean moth counts at 150 to 600 m from treated plots (distance classes 3 and 4) were significantly lower ($P < 0.05$) than at distances > 600 m (Fig. 3A). In lines of traps across the valley, the mean moth counts at 50

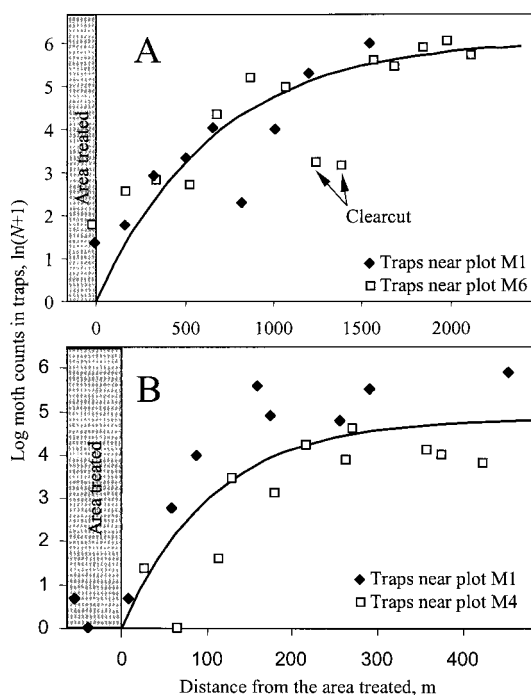


Fig. 2. Log-transformed male gypsy moth capture in individual pheromone traps along the valley (A) near plots M1 and M6, and across the valley near plots M1 and M4 in 2000 and its relationship to the distance from the nearest treated plot. Nonlinear regression: (A) $\ln(N + 1) = 6.02[1 - \exp(-3x/1899)]$; (B) $\ln(N + 1) = 4.86[1 - \exp(-3x/312)]$.

to 150 m from treated plots (distance class 2) were significantly lower ($P < 0.05$) than those at distances > 150 m (Fig. 3B).

In 2001, moth counts in traps increased with increasing distance from the area treated (Fig. 4). Nonlinear regression (equation 1) indicates that this relationship is statistically significant ($R^2 = 0.38$; $F = 23.6$; $df = 1, 38$; $P < 0.001$). The range of disparlure effect on moth capture was shorter ($b = 200 \pm 51$ m, \pm SE) than along the valley in 2000, but similar to the range across the valley in 2000.

The GLM analysis of 2001 data indicated a significant effect of distance from treated area on moth counts in lines of traps (Table 1; Fig. 3C). The mean moth counts at 50–150 m from treated plots (distance class 2) were significantly lower ($P < 0.05$) than at distances > 600 m.

In all experiments, moth counts in pheromone traps were lower near treated plots than farther away. This indicates that male search behavior is affected by disparlure beyond the boundary of these plots. This effect usually was limited to 150 to 250 m from the plot. However, in the narrow valley at Millboro Springs, the effect of disparlure was observed 600 m away from the treated area.

Effect of Disparlure on the Recapture Rate of Released Male Moths Outside of Treated Areas. According to the GLM analysis, the rate of male moth recap-

Table 1. General linear model (GLM) analysis of log-transformed counts of feral male moths in pheromone traps per season at various distances from plots treated with disparlure

Geographic location	Year	Source	df	Sum of squares	Adjusted M.S.	F	P
Millboro Springs along the valley	2000	Distance class ^a	4	39.59	9.897	22.83	<0.001
		Line of traps	1	4.81	1.189	3.46	0.082
		Error	15	5.03	0.360		
		Total	20	49.55			
Millboro Springs across the valley	2000	Distance class	3	55.24	18.414	23.11	<0.001
		Line of traps	1	0.74	6.012	7.55	0.014
		Error	16	12.75	0.797		
		Total	20	68.73			
Goshen	2001	Distance class	4	12.98	3.245	10.14	<0.001
		Line of traps	1	0.01	0.007	0.02	0.884
		Error	34	10.88	0.320		
		Total	39	23.87			

^a Distance classes are: <50, 50–150, 150–250, 250–600, 600–1200, and >1200 m from treated areas.

ture increased with increasing distance from treated plots in Millboro Springs in 2000, in Goshen in 2001, and in Buckingham-Appomattox State Forest in 2001 (Fig. 5; Table 2). In all three locations, moth recapture rates at distances of 50 to 150 m from the treated area were significantly lower ($P < 0.05$) than those at distances >250 m. This is additional evidence that disparlure disperses from treated plots and affects male moth behavior beyond the plot boundary.

Effect of Disparlure on Mating Success of Females Outside of Treated Areas. The fertilization status of most tethered females was clearly identified. From 552 females analyzed there were only six possibly unfertilized females that did not lay any eggs and 6 possibly fertilized females that had 1 to 2 embryonated eggs in their egg mass. The two methods for estimating the proportion of fertilization were highly correlated ($r = 0.9994$). Thus, in all results below we used only the former estimate of the proportion of fertilized females without considering those few females whose fertilization status was not clear.

The proportion of fertilized females increased with increasing distance from treated plots (Fig. 6). Re-

duced mating success of tethered females was observed up to 800 m from the boundary of the treated area.

The proportion of fertilized females in each line of females was closely related to the moth capture rate in nearby pheromone traps (Fig. 7). The relationship between the proportion of fertilized females and male moth capture in pheromone traps was modeled by equation 2. The relative search rate was $s = 0.23 \pm 0.025$ (\pm SE).

Earlier studies of the relationship between male moth capture rate in pheromone traps and mating success of females in areas treated with disparlure showed that male moth capture in traps was reduced to a greater extent than the mating probability of females (Schwalbe and Mastro 1988, Kolodny-Hirsch and Webb 1993). Thus, traps were not considered reliable enough for evaluating the results of mating disruption treatments. Our experiment revealed a strong relationship between mating success of tethered females in the area affected by disparlure and moth counts in pheromone traps. However, all earlier experiments, where disparlure did reduce moth

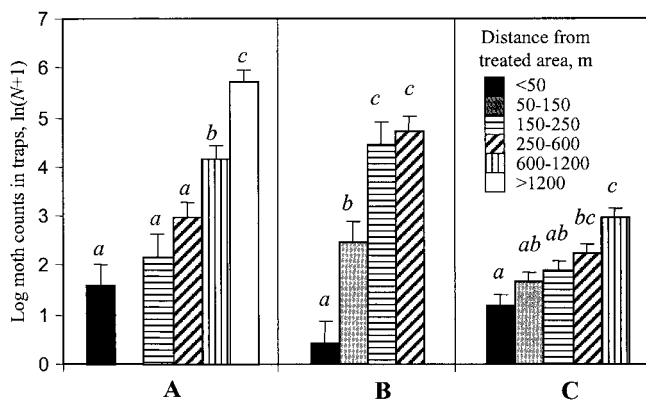


Fig. 3. Mean log-transformed male gypsy moth capture per trap per season in lines of traps along the valley at various distances from plots M1 and M6 treated with disparlure in 2000 (A), or across the valley from plots M1 and M4 in 2000 (B), and from plot G1 in 2001 (C). Means and standard errors were generated using the General Linear model (GLM) with the following two factors: distance class and line of traps. A difference between bars (within each of the three groups) is not significant ($P > 0.05$) if marked by the same character (multiple comparison, Tukey's method).

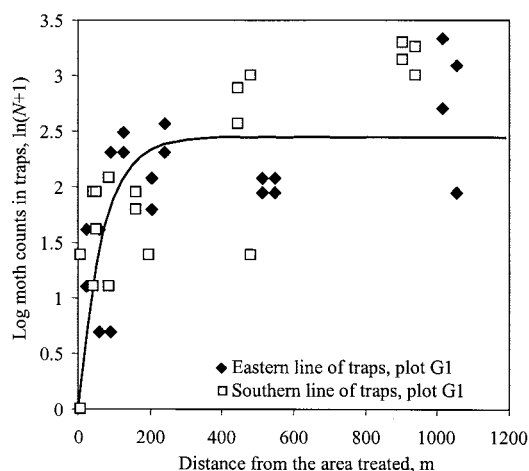


Fig. 4. Log-transformed male gypsy moth capture in individual pheromone traps near plot G1 in 2001 and its relationship to the distance from the nearest plot; non-linear regression: $\ln(N + 1) = 2.45[1 - \exp(-3x/200)]$.

counts in traps but did not sufficiently reduce female mating probability, were done in high-density populations. For example, in the experiments by Schwalbe and Mastro (1988), daily moth captures per trap reached 100, which corresponds to ≈ 2000 moths per season. The relationship between moth counts in traps and mating success of females becomes saturated if moth counts per day are >10 (Fig. 7). According to the model, a reduction in moth counts in traps from 100 to 10 per day only corresponds to a reduction in the probability of mating from 100 to 90%.

Sharov et al. (1995) quantified the relationship between counts of gypsy moths in traps and mating success of females in nontreated areas; thus, it was interesting to compare these data with our results obtained in an area affected by disparlure. According to Sharov et al. (1995), the relative search rate of male moths in nontreated areas was $s = 0.15 \pm 0.04$, \pm SE

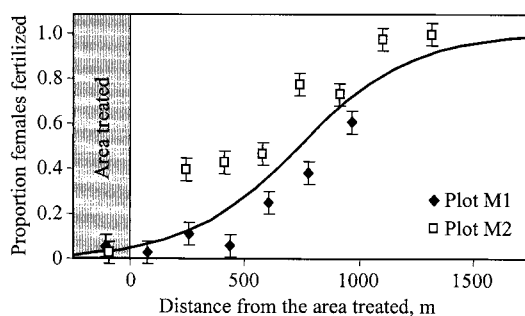


Fig. 6. Mating success of tethered gypsy moth females at various distances along the valley from the nearest plot treated with disparlure.

Although it is slightly lower than the value of parameter s estimated in this study in areas affected by disparlure, the difference is not significant ($t = 1.70$, $df = 34$, $P > 0.05$). A similar experiment in Wisconsin in 2000 yielded an estimate of $s = 0.22$ (A.S. and K.T., unpublished) which is even closer to the value obtained in this study.

Both mating success of females and the catch rate of pheromone traps decreased near treated blocks. However, the ratio of probability of a male to copulate with a female to the probability of entering a trap, s , remained the same, as follows from the good fit of the model (equation 2) to field data (Fig. 7). Thus, trap catches can be used to predict mating success in and near areas treated with disparlure. Of course, predictions should take into account additional factors, such as the spatial distribution of females and the effect of delayed mating. If not mated within 1 d, waiting females can be eaten by ants (Sharov et al. 1995). A small proportion of females may be located in sites not visited by ants, providing a longer opportunity for discovery by male moths, and thus have a higher chance of getting fertilized. Unmated females often start depositing unfertilized eggs; then if mated they

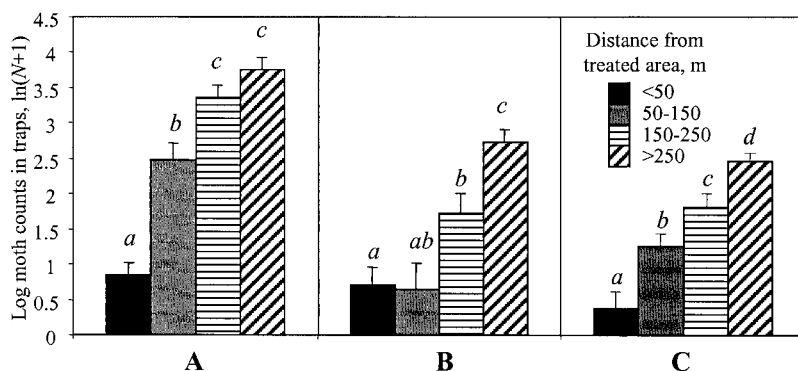


Fig. 5. Mean log-transformed male gypsy moth recapture per release site (four traps) per week at various distances from areas treated with disparlure: plots M1, M4, and M6 in 2000 (A), plot G1 in 2001 (B), and plots BA1 and C1 in 2001 (C). Means and standard errors were generated using the General Linear model (GLM) with the following three factors: distance class, line of release-recapture sites, and week. A difference between bars in each group is not significant ($P > 0.05$) if marked with the same character (multiple comparison, Tukey's method).

Table 2. General linear model (GLM) analysis of log-transformed weekly gypsy moth recapture rates of male moths released at various distances from plots treated with disparlure

Geographic location	Year	Source	df	Sum of squares	Adjusted M.S.	F	P
Millboro Springs	2000	Distance class ^a	3	59.58	19.91	52.56	<0.001
		Line of sites	5	10.24	2.05	5.40	0.001
		Week	1	0.03	0.03	0.08	0.777
		Error	34	12.88	0.38		
		Total	43	82.73			
Goshen	2001	Distance class	3	28.20	9.35	17.56	<0.001
		Line of sites	1	0.04	0.04	0.08	0.777
		Week	3	8.57	2.86	5.36	0.005
		Error	28	14.91	0.53		
		Total	35	51.73			
Buckingham-Appomattox and Cumberland State Forests	2001	Distance class	3	54.79	18.26	30.19	<0.001
		Line of sites	3	9.38	0.45	0.74	0.528
		Week	7	28.13	3.93	6.50	<0.001
		Error	98	59.28	0.60		
		Total	111	151.57			

^a Distance classes are: <50, 50–150, 150–250, and >250 m from treated areas.

have a reduced ability to deposit fertile eggs (Richerson et al. 1976b). Another limitation for the use of equation 2 is that population density should be relatively low. In high-density populations, the relationship between female mating success and male moth capture rate in pheromone traps may be different, because males are so abundant that some of them may be able to find females by short-range search.

This paper presents the first evidence of a long-range effect of synthetic pheromones used for mating disruption on moth capture rates in pheromone traps and on the mating success of females. The effect of synthetic pheromones used for mating disruption has been viewed as a local treatment similar to a pesticide application. This paper shows strong nonlocal effects at distances up to 250 to 600 m from treated areas. This finding may change the strategy of pheromone application in the future; for example, it may be possible to increase the width of airplane swaths in mating disruption treatments and hence reduce application costs. However, determining the acceptable width of gaps between treated swaths requires additional research.

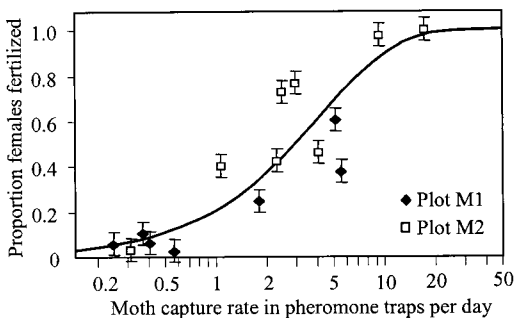


Fig. 7. The relationship between mating success of tethered gypsy moth females located at various distances from treated plots and average moth capture rate in two adjacent traps during the same time.

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